be added, however, that the contents of the only volume as yet published refer chiefly to the historical development of geographical discovery in China and Central Asia, forming by far the most copious and thoroughly digested summary of facts ever as yet presented relating to this interesting but difficult subject.

THE COLORS OF ANIMALS AND PLANTS.[1]

BY ALFRED RUSSEL WALLACE.

I. THE COLORS OF ANIMALS.

Theory of Sexual Colors. — In Mr. Darwin's celebrated work, The Descent of Man and Selection in Relation to Sex, he has treated of sexual color in combination with other sexual characters, and has arrived at the conclusion that all, or almost all, the colors of the higher animals (including among these insects and all vertebrates) are due to voluntary sexual selection; and that diversity of color in the sexes is due, primarily, to the transmission of color-variations either to one sex only, or to both sexes, the difference depending on some unknown law, and not being due to natural selection.

I have long held this portion of Mr. Darwin's theory to be erroneous, and have argued that the primary cause of sexual diversity of color was the need of protection, repressing in the female those bright colors which are nominally produced in both sexes by general laws; and I have attempted to explain many of the more difficult cases on this principle (A Theory of Birds' Nests, in Contributions, etc., page 231). As I have since given much thought to this subject, and have arrived at some views which appear to me to be of considerable importance, it will be well to sketch briefly the theory I now hold, and afterward show its application to some of the detailed cases adduced in Mr Darwin's work.

The very frequent superiority of the male bird or insect in brightness or intensity of color, even when the general tints and coloration are the same, now seems to me to be due to the greater vigor and activity and the higher vitality of the male. The colors of an animal usually fade during disease or weakness, while robust health and vigor add to their intensity. This intensity of coloration is most manifest in the male during the breeding-season, when the vitality is at a maximum. It is also very manifest

[1] From Macmillan's Magazine. Concluded from page 662.

in those cases in which the male is smaller than the female, as in the hawks and in most butterflies and moths. The same phenomena occur, though in a less marked degree, among mammalia. Whenever there is a difference of color between the sexes the male is the darker or more strongly marked, and difference of intensity is most visible during the breeding season (Descent of Man, page 533). Numerous cases among domestic animals also prove that there is an inherent tendency in the male to special developments of dermal appendages and color, quite independently of sexual or any other form of selection. Thus, "the hump on the male zebu cattle of India, the tail of fat-tailed rams, the arched outline of the forehead in the males of several breeds of sheep, and the mane, the long hairs on the hind-legs, and the dewlap of the male of the Berbura goat," are all adduced by Mr. Darwin as instances of characters peculiar to the male, yet not derived from any parent ancestral form. Among domestic pigeons the character of the different breeds is often most strongly manifested in the male birds; the wattle of the carriers and the eye-wattles of the barbs are largest in the males, and male pouters distend their crops to a much greater extent than do the females, and the cock fantails often have a greater number of tail-feathers than the females. There are also some varieties of pigeons of which the males are striped or spotted with black, while the females are never so spotted (Animals and Plants under Domestication, i., 161); yet in the parent stock of these pigeons there are no differences between the sexes either of plumage or color, and artificial selection has not been applied to produce them.

The greater intensity of coloration in the male — which may be termed the normal sexual difference — would be further developed by the combats of the males for the possession of the females. The most vigorous and energetic usually being able to rear most offspring, intensity of color, if dependent on or correlated with vigor, would tend to increase. But as differences of color depend upon minute chemical or structural differences in the organism, increasing vigor acting unequally on different portions of the integument, and often producing at the same time abnormal developments of hair, horns, scales, feathers, etc., would almost necessarily lead also to variable distribution of color, and thus to the production of new tints and markings. These acquired colors would, as Mr. Darwin has shown, be transmitted to both sexes or to one only, according as they first ap-

peared at an early age, or in adults of one sex, and thus we may account for some of the most marked differences in this respect. With the exception of butterflies, the sexes are almost alike in the great majority of insects. The same is the case in mammals and reptiles, while the chief departure from the rule occurs in birds, though even here in very many cases the law of sexual likeness prevails. But in all cases where the increasing development of color became disadvantageous to the female, it would be checked by natural selection, and thus produce those numerous instances of protective coloring in the female only which occur in these two groups of animals.

There is also, I believe, a very important purpose and use of the varied colors of the higher animals, in the facility it affords for recognition by the sexes or by the young of the same species; and it is this use which probably fixes and determines the coloration in many cases. When differences of size and form are very slight, color affords the only means of recognition at a distance or while in motion, and such a distinctive character must therefore be of especial value to flying insects which are continually in motion, and encounter each other, as it were, by accident. This view offers us an explanation of the curious fact that among butterflies the females of closely-allied species in the same locality sometimes differ considerably, while the males are much alike; for as the males are the swiftest and the highest fliers and seek the females, it would evidently be advantageous for them to be able to recognize their true partners at some distance off. This peculiarity occurs with many species of *Papilio*, *Diadema*, *Adolias*, and *Colias*. In birds such marked differences of color are not required, owing to their higher organization and more perfect senses, which render recognition easy by means of a combination of very slight differential characters. This principle may, perhaps, however, account for some anomalies of coloration among the higher animals. Thus, Mr. Darwin, while admitting that the hare and the rabbit are colored protectively, remarks that the latter, while running to its burrow, is made conspicuous to the sportsman, and no doubt to all beasts of prey, by its upturned, white tail. But this very conspicuousness while running away may be useful as a signal and guide to the young, who are thus enabled to escape danger by following the older rabbits, directly and without hesitation, to the safety of the burrow; and this may be the more important from the semi-nocturnal habits of the animal. If this explanation is correct, and it certainly seems prob-

able, it may serve as a warning of how impossible it is, without exact knowledge of the habits of an animal and a full consideration of all the circumstances, to decide that any particular coloration cannot be protective or in any way useful. Mr. Darwin himself is not free from such assumptions. Thus, he says: "The zebra is conspicuously striped, and stripes cannot afford any protection on the open plains of South Africa." But the zebra is a very swift animal, and, when in herds, by no means void of means of defense. The stripes, therefore, *may* be of use by enabling stragglers to distinguish their fellows at a distance, and they *may* be even protective when the animal is at rest among herbage — the only time when it would need protective coloring. Until the habits of the zebra have been observed with special reference to this point, it is surely somewhat hasty to declare that the stripes "cannot afford any protection."

The wonderful display and endless variety of color in which butterflies and birds so far exceed all other animals seem primarily due to the excessive development and endless variations of the integumentary structures. No insects have such widely-expanded wings in proportion to their bodies as butterflies and moths; in none do the wings vary so much in size and form, and in none are they clothed with such a beautiful and highly-organized coating of scales. According to the general principles of the production of color already explained, these long-continued expansions of membranes and developments of surface-structures must have led to numerous color-changes, which have been sometimes checked, sometimes fixed and utilized, sometimes intensified, by natural selection, according to the needs of the animal. In birds, too, we have the wonderful clothing of plumage — the most highly-organized, the most varied, and the most expanded of all dermal appendages. The endless processes of growth and change during the development of feathers, and the enormous extent of this delicately-organized surface, must have been highly favorable to the production of varied color-effects, which, when not injurious, have been merely fixed for purposes of specific identification, but have often been modified or suppressed whenever different tints were needed for purposes of protection.

To voluntary sexual selection, that is, the actual choice by the females of the more brilliantly-colored males, I believe very little if any effect is directly due. It is undoubtedly proved that in birds the females do sometimes exert a choice; but the evidence of this fact collected by Mr. Darwin (Descent of Man, chapter

xiv.) does not prove that color determines that choice, while much of the strongest evidence is directly opposed to this view. All the facts appear to be consistent with the choice depending on a variety of male characteristics, with some of which color is often correlated. Thus it is the opinion of some of the best observers that vigor and liveliness are most attractive, and these are, no doubt, usually associated with intensity of color. Again, the display of the various ornamental appendages of the male during courtship may be attractive; but these appendages, with their bright colors or shaded patterns, are due probably to general laws of growth and to that superabundant vitality which we have seen to be a cause of color. But there are many considerations which seem to show that the possession of these ornamental appendages and bright colors in the male is not an important character functionally, and that it has not been produced by the action of voluntary sexual selection. Amid the copious mass of facts and opinions collected by Mr. Darwin as to the display of color and ornaments by the male birds, there is a total absence of any evidence that the females admire or even notice this display. The hen, the turkey, and the pea-fowl, go on feeding while the male is displaying his finery, and there is reason to believe that it is his persistency and energy rather than his beauty which wins the day. Again, evidence collected by Mr. Darwin himself proves that each bird finds a mate under any circumstances. He gives a number of cases of one of a pair of birds being shot, and the survivor being always found paired again almost immediately. This is sufficiently explained on the assumption that the destruction of birds by various causes is continually leaving widows and widowers in nearly equal proportions, and thus each one finds a fresh mate; and it leads to the conclusion that permanently-unpaired birds are very scarce; so that, speaking broadly, every bird finds a mate and breeds. But this would almost or quite neutralize any effect of sexual selection of color or ornament, since the less highly-colored birds would be at no disadvantage as regards leaving healthy offspring. If, however, heightened color is correlated with health and vigor, and these healthy and vigorous birds provide best for their young, and leave offspring which, being equally healthy and vigorous, can best provide for themselves, then natural selection becomes a preserver and intensifier of color. Another most important consideration is, that male butterflies rival or even excel the most gorgeous male birds in bright colors and elegant patterns; and

among these there is literally not one particle of evidence that the female is influenced by color, or even that she has any power of choice, while there is much direct evidence to the contrary (Descent of Man, page 318). The weakness of the evidence for sexual selection among these insects is so palpable that Mr. Darwin is obliged to supplement it by the singularly inconclusive argument that "unless the females prefer one male to another, the pairing must be left to mere chance, and this does not appear probable" (*loc. cit.*, page 317). But he has just said, "The males sometimes fight together in rivalry, and many may be seen pursuing or crowding round the same female;" while in the case of the silk-moths, "the females appear not to evince the least choice in regard to their partners." Surely, the plain inference from all this is, that males fight and struggle for the almost passive female, and that the most vigorous and energetic, the strongest-winged or the most persevering, wins her. How can there be chance in this? Natural selection would here act, as in birds, in perpetuating the strongest and most vigorous males, and as these would usually be the more highly-colored of their race, the same results would be produced as regards the intensification and variation of color in the one case as in the other.

Let us now see how these principles will apply to some of the cases adduced by Mr. Darwin in support of his theory of voluntary sexual selection.

In Descent of Man, second edition, pp. 307–316, we find an elaborate account of the various modes of coloring of butterflies and moths, proving that the colored parts are always more or less displayed, and that they have some evident relation to an observer. Mr. Darwin then says: "From the several foregoing facts it is impossible to admit that the brilliant colors of butterflies, and of some few moths, have commonly been acquired for the sake of protection. We have seen that their colors and elegant patterns are arranged and exhibited as if for display. Hence, I am led to believe that the females prefer or are most excited by the more brilliant males; for on any other supposition the males would, as far as we can see, be ornamented to no purpose" (*loc. cit.*, p. 316). I am not aware that any one has ever maintained that the brilliant colors of butterflies have "commonly been acquired for the sake of protection," yet Mr. Darwin has himself referred to cases in which the brilliant color is so placed as to serve for protection; as, for example, the eye-spots on the hind-wings of moths, which are pierced by birds, and

so save the vital parts of the insect, while the bright patch on the orange-tip butterflies, which Mr. Darwin denies are protective, may serve the same purpose. It is, in fact, somewhat remarkable how very generally the black spots, ocelli, or bright patches of color, are on the tips, margins, or disks of the wings; and, as the insects are necessarily visible while flying, and this is the time when they are most subject to attacks by insectivorous birds, the position of the more conspicuous parts at some distance from the body may be a real protection to them. Again, Mr. Darwin admits that the white color of the male ghost-moth may render it more easily seen by the female while flying about in the dusk, and if to this we add that it will be also more readily distinguished from allied species, we have a reason for diverse ornamentation in these insects quite sufficient to account for most of the facts, without believing in the selection of brilliant males by the females, for which there is not a particle of evidence. The facts given to show that butterflies and other insects can distinguish colors, and are attracted by colors similar to their own, are quite consistent with the view that color, which continually tends to appear, is utilized for purposes of identification and distinction, when not required to be modified or suppressed for purposes of protection. The cases of the females of some species of *Thecla*, *Callidryas*, *Colias*, and *Hipparchia*, which have more conspicuous markings than the male, may be due to several causes: to obtain greater distinction from other species, for protection from birds, as in the case of the yellow-under-wing moths, while sometimes—as in *Hipparchia*—the lower intensity of coloring in the female may lead to more contrasted markings. Mr. Darwin thinks that here the males have selected the more beautiful females, although one chief fact in support of his theory of voluntary sexual selection is, that throughout the whole animal kingdom the males are usually so ardent that they will accept any female, while the females are coy, and choose the handsomest males, whence it is believed the general brilliancy of males as compared with females has arisen.

Perhaps the most curious cases of sexual difference of color are those in which the female is very much more gayly colored than the male. This occurs most strikingly in some species of *Pieris* in South America, and of *Diadema* in the Malay islands, and in both cases the females resemble the uneatable Danaidæ and Heliconidæ, and thus gain a protection. In the case of *Pieris pyrrha*, *P. malenka*, and *P. lorena*, the males are plain white

and black, while the females are orange, yellow, and black, and so banded and spotted as exactly to resemble species of Heliconidæ. Mr. Darwin admits that these females have acquired these colors as a protection; but as there is no apparent cause for the strict limitation of the color to the female, he believes that it has been kept down in the male by its being *unattractive* to her. This appears to me to be a supposition opposed to the whole theory of sexual selection itself. For this theory is, that minute variations of color in the male are *attractive* to the female, have always been selected, and that thus the brilliant male colors have been produced. But in this case he thinks that the female butterfly had a constant aversion to every trace of color, even when we must suppose it was constantly recurring during the successive variations which resulted in such a marvelous change in herself. But if we consider the fact that the females frequent the forests where the Heliconidæ abound, while the males fly much in the open, and assemble in great numbers with other white and yellow butterflies on the banks of rivers, may it not be possible that the appearance of orange stripes or patches would be as injurious to the male as it is useful to the female, by making him a more easy mark for insectivorous birds among his white companions? This seems a more probable supposition than the altogether hypothetical choice of the female, sometimes exercised in favor of and sometimes against every new variety of color in her partner.

The full and interesting account given by Mr. Darwin of the colors and habits of male and female birds (Descent of Man, chapters xiii. and xiv.) proves that in most, if not in all, cases the male birds fully display their ornamental plumage before the females, and in rivalry with each other; but on the essential point of whether the female's choice is determined by minute differences in these ornaments or in their colors, there appears to be an entire absence of evidence. In the section on Preference for Particular Males by the Females, the facts quoted show indifference to color, except that some color similar to their own seems to be preferred. But in the case of the hen-canary, who chose a greenfinch in preference to either chaffinch or goldfinch, gay colors had evidently no preponderating attraction. There is some evidence adduced that female birds may, and probably do, choose their mates, but none whatever that the choice is determined by difference of color; and no less than three eminent breeders informed Mr. Darwin that they "did not believe that

the females prefer certain males on account of the beauty of their plumage." Again, Mr. Darwin himself says, "As a general rule, color appears to have little influence on the pairing of pigeons." The oft-quoted case of Sir R. Heron's peahens, which preferred an "old pied cock" to those normally colored, is a very unfortunate one, because pied birds are just those that are not favored in a state of nature, or the breeds of wild birds would become as varied and mottled as our domestic varieties. If such irregular fancies were not rare exceptions, the production of definite colors and patterns by the choice of the female birds, or in any other way, would be impossible.

We now come to such wonderful developments of plumage and color as are exhibited by the peacock and the Argus pheasant; and I may here mention that it was the latter bird, as fully discussed by Mr. Darwin, which first shook my belief in "sexual," or more properly "female," selection. The long series of gradations by which the beautifully-shaded ocelli on the secondary wing feathers of this bird have been produced are clearly traced out, the result being a set of markings so exquisitely shaded as to represent "balls lying loose within sockets," — purely artificial objects of which these birds could have no possible knowledge. That this result should have been attained through thousands and tens of thousands of female birds, all preferring those males whose markings varied slightly in this one direction, this uniformity of choice continuing through thousands and tens of thousands of generations, is to me absolutely incredible. And when, further, we remember that those which did not so vary would also, according to all the evidence, find mates and leave offspring, the actual result seems quite impossible of attainment by such means.

Without pretending to solve completely so difficult a problem, I would point out a circumstance which seems to afford a clew. It is that the most highly colored and most richly varied markings occur on those parts of the plumage which have undergone the greatest modification, or have acquired the most abnormal development. In the peacock the tail coverts are enormously developed, and the "eyes" are situated on the greatly dilated ends. In the birds-of-paradise, breast, or neck, or head, or tail feathers are greatly developed and highly colored. The hackles of the cock and the scaly breasts of humming-birds are similar developments; while in the Argus pheasant the secondary quills are so enormously lengthened and broadened as to have become almost useless for flight. Now, it is easily conceivable that, dur-

ing this process of development, inequalities in the distribution of color may have arisen in different parts of the same feather, and that spots and bands may thus have become broadened out into shaded spots or ocelli, in the way indicated by Mr. Darwin, much as the spots and rings on a soap-bubble increase with increasing tenuity. This is the more probable, as in domestic fowls varieties tend to become symmetrical, quite independently of sexual selection. (Descent of Man, page 424.)

If, now, we accept the evidence of Mr. Darwin's most trustworthy correspondents that the choice of the female, so far as she exerts any, falls upon the "most vigorous, defiant, and mettlesome male," and if we further believe, what is certainly the case, that these are, as a rule, the most brightly colored and adorned with the finest developments of plumage, we have a real and not a hypothetical cause at work. For these most healthy, vigorous, and beautiful males will have the choice of the finest and most healthy females, will have the most numerous and healthy families, and will be able best to protect and rear those families. Natural selection, and what may be termed male selection, will tend to give them the advantage in the struggle for existence, and thus the fullest plumage and the finest colors will be transmitted, and tend to advance in each succeeding generation.

There remains, however, what Mr. Darwin evidently considers his strongest argument, the display by the male of each species of its peculiar beauties of plumage and color. We have here, no doubt, a very remarkable and very interesting fact; but this, too, may be explained by general principles, quite independent of any choice or volition of the female bird. During pairing-time the male bird is in a state of great excitement, and full of exuberant energy. Even unornamented birds flutter their wings or spread them out, erect their tails or crests, and thus give vent to the nervous excitability with which they are overcharged. It is not improbable that crests and other erectile feathers may be primarily of use in frightening away enemies, since they are generally erected when angry or during combat. Those individuals who were most pugnacious and defiant, and who brought these erectile plumes most frequently and most powerfully into action, would tend to increase them by use, and to leave them further developed in some of their descendants. If, in the course of this development, color appeared, we have every reason to believe it would be most vivid in these most pugnacious and energetic individuals; and as these would always have the advantage in the

rivalry for mates (to which advantage the excess of color and plumage might sometimes conduce), there seems nothing to prevent a progressive development of these ornaments in *all dominant races*, that is, wherever there was such a surplus of vitality and such complete adaptation to conditions that the inconvenience or danger produced by them was so comparatively small as not to affect the superiority of the race over its nearest allies. If, then, those portions of the plumage which were originally erected and displayed became developed and colored, the actual display, under the influence of jealousy or sexual excitement, becomes intelligible. The males, in their rivalry with each other, would see what plumes were most effective, and each would endeavor to excel his enemy as far as voluntary exertion could effect it, just as they endeavor to rival each other in song, even sometimes to the point of causing their own destruction.

There is also a general argument against Mr. Darwin's views on this question, founded on the nature and potency of "natural" as opposed to "sexual" selection, which appears to me to be itself almost conclusive of the whole matter at issue. Natural selection, or the survival of the fittest, acts perpetually and on an enormous scale. Taking the offspring of each pair of birds as, on the average, only six annually, one third of these at most will be preserved, while the two thirds which are least fitted will die. At intervals of a few years, whenever unfavorable conditions occur, five sixths, nine tenths, or even a greater proportion of the whole yearly production are weeded out, leaving only the most perfect and best adapted to survive. Now, unless these survivors are on the whole the most ornamental, this rigid selective power must neutralize and destroy any influence that may be exerted by female selection. For the utmost that can be claimed for this is that a small fraction of the least ornamented do not obtain mates, while a few of the most ornamented may leave more than the average number of offspring. Unless, therefore, there is the strictest correlation between ornament and general perfection, the former can have no permanent advantage; and if there is (as I maintain) such a correlation, then the sexual selection of ornament, for which there is little or no evidence, becomes needless, because natural selection, which is an admitted *vera causa*, will itself produce all the results. In the case of butterflies the argument becomes even stronger, because the fertility is so much greater, and the weeding out of the unfit takes place, to a great extent, in the egg and larva state. Unless the eggs and larvæ

which escaped to produce the next generation were those which would produce the more highly colored butterflies, it is difficult to perceive how the slight preponderance of color sometimes selected by the females should not be wholly neutralized by the extremely rigid selection for other qualities to which the offspring in every stage are exposed. The only way in which we can account for the observed facts is by the supposition that color and ornament are strictly correlated with health, vigor, and general fitness to survive. We have shown that there is reason to believe that this is the case, and, if so, voluntary sexual selection becomes as unnecessary as it would certainly be ineffective.

There is one other very curious case of sexual coloring among birds: that, namely, in which the female is decidedly brighter or more strongly marked than the male, as in the fighting quails (*Turnix*), painted snipe (*Rhynchœa*), two species of phalarope (*Phalaropus*), and the common cassowary (*Casuarius galeatus*). In all these cases, it is known that the males take charge of and incubate the eggs, while the females are almost always larger and more pugnacious. In my Theory of Birds' Nests [1] I imputed this difference of color to the greater need for protection by the male bird while incubating, to which Mr. Darwin has objected that the difference is not sufficient, and is not always so distributed as to be most effective for this purpose; and he believes that it is due to reversed sexual selection, that is, to the female taking the usual *rôle* of the male, and being chosen for her brighter tints. We have already seen reason for rejecting this latter theory in every case, and I also admit that my theory of protection is, in this case, only partially, if at all, applicable. But the general theory of intensity of color being due to general vital energy is quite applicable; and the fact that the superiority of the female in this respect is quite exceptional, and is therefore probably not of very ancient date in any one case, will account for the difference of color thus produced being always comparatively slight.

Theory of Typical Colors. — The remaining kinds of animal colors — those which can neither be classed as protective, warning, nor sexual — are for the most part readily explained on the general principles of the development of color which we have now laid down. It is a most suggestive fact that, in cases where color is required only as a warning, as among the uneatable caterpillars, we find, not one or two glaring tints only, but every kind of color disposed in elegant patterns, and exhibiting almost

[1] Natural Selection, page 251.

as much variety and beauty as among insects and birds. Yet here, not only is sexual selection out of the question, but the need for recognition and identification by others of the same species seems equally unnecessary. We can then only impute this variety to the normal production of color in organic forms, when fully exposed to light and air and undergoing great and rapid developmental modification. Among more perfect animals, where the need for recognition has been added, we find intensity and variety of color at its highest pitch among the South American butterflies of the families Heliconidæ and Danaidæ, as well as among the Nymphalidæ and Erycinidæ, many of which obtain the necessary protection in other ways. Among birds, also, wherever the habits are such that no special protection is needed for the females, and where the species frequent the depths of tropical forests, and are thus naturally protected from the swoop of birds of prey, we find almost equally intense coloration, as in the trogons, barbets, and gapers.

Of the mode of action of the general principles of color development among animals, we have an excellent example in the humming-birds. Of all birds these are at once the smallest, the most active, and the fullest of vital energy. When poised in the air, their wings are invisible, owing to the rapidity of their motion, and when startled they dart away with the rapidity of a flash of light. Such active creatures would not be an easy prey to any rapacious bird; and if one at length was captured, the morsel obtained would hardly repay the labor. We may be sure, therefore, that they are practically unmolested. The immense variety they exhibit in structure, plumage, and color indicates a high antiquity for the race, while their general abundance in individuals shows that they are a dominant group, well adapted to all the conditions of their existence. Here we find everything necessary for the development of color and accessory plumes. The surplus vital energy shown in their combats and excessive activity has expended itself in ever-increasing developments of plumage and greater and greater intensity of color, regulated only by the need for specific identification, which would be especially required in such small and mobile creatures. Thus may be explained those remarkable differences of color between closely-allied species, one having a crest like the topaz, while in another it resembles the sapphire. The more vivid colors and more developed plumage of the males, I am now inclined to think, may be wholly due to their greater vital energy and to

those general laws which lead to such superior developments even in domestic breeds; but in some cases the need of protection by the female while incubating, to which I formerly imputed the whole phenomenon, may have suppressed a portion of the ornament which she would otherwise have attained.

Another real though as yet inexplicable cause of diversity of color is to be found in the influence of locality. It is observed that species of totally distinct groups are colored alike in one district, while in another district the allied species all undergo the same change of color. Cases of this kind have been adduced by Mr. Bates, by Mr. Darwin, and by myself, and I have collected all the more curious and important examples in my Address to the Biological Section of the British Association at Glasgow in 1876. The most probable cause for these simultaneous variations would seem to be the presence of peculiar elements or chemical compounds in the soil, the water, or the atmosphere, or of special organic substances in the vegetation; and a wide field is thus offered for chemical investigation in connection with this interesting subject. Yet, however we may explain it, the fact remains of the same vivid colors in definite patterns being produced in quite unrelated groups, which only agree, so far as we yet know, in inhabiting the same locality.

Let us now sum up the conclusion at which we have arrived as to the various modes in which color is produced or modified in the animal kingdom.

The various causes of color in the animal world are molecular and chemical change of the substance of their integuments, or the action on it of heat, light, or moisture. It is also produced by interference of light in superposed transparent lamellæ, or by excessively fine surface striæ. These elementary conditions for the production of color are found everywhere in the surface structures of animals, so that its presence must be looked upon as normal, its absence as exceptional.

Colors are fixed or modified in animals by natural selection for various purposes: obscure or imitative colors for concealment; gaudy colors as a warning; and special markings either for easy recognition by strayed individuals, females, or young, or to direct attack from a vital part, as in the large, brilliantly-marked wings of some butterflies and moths.

Colors are produced or intensified by processes of development, — either where the integument or its appendages undergo great extension or modification, or where there is a surplus of

vital energy, as in male animals generally, and more especially at the breeding-season.

Colors are also more or less influenced by a variety of causes, such as the nature of the food, the photographic action of light, and also by some unknown local action probably dependent on chemical peculiarities in the soil or vegetation.

These various causes have acted and reacted in a variety of ways, and have been modified by conditions dependent on age or on sex, on competition with new forms or on geographical or climatic changes. In so complex a subject, for which experiment and systematic inquiry have done so little, we cannot expect to explain every individual case, or solve every difficulty; but it is believed that all the great features of animal coloration and many of the details become explicable on the principles we have endeavored to lay down.

It will perhaps be considered presumptuous to put forth this sketch of the subject of color in animals as a substitute for one of Mr. Darwin's most highly elaborated theories, — that of voluntary or perceptive sexual selection, — yet I venture to think that it is more in accordance with the whole of the facts, and with the theory of natural selection itself; and I would ask such of my readers as may be sufficiently interested in the subject to read again chapters xi. to xvi. of the Descent of Man, and consider the whole theory from the point of view here laid down.

The explanation of almost all the ornaments and colors of birds and insects as having been produced by the perceptions and choice of the females has, I believe, staggered many evolutionists, but has been provisionally accepted, because it was the only theory that even attempted to explain the facts. It may perhaps be a relief to some of them, as it has been to myself, to find that the phenomena can be shown to depend on the general laws of development and on the action of "natural selection," which theory will, I venture to think, be relieved from an abnormal excrescence, and gain additional vitality by the adoption of my view of the subject.

Although we have arrived at the conclusion that tropical light and heat can in no sense be considered the cause of color, there remains to be explained the undoubted fact that all the more intense and gorgeous tints are manifested by the animal life of the tropics, while in some groups, such as butterflies and birds, there is a marked preponderance of highly colored species. This is probably due to a variety of causes, some of which we can indi-

cate, while others remain to be discovered. The luxuriant vegetation of the tropics throughout the entire year affords so much concealment that color may there be safely developed to a much greater extent than in climates where the trees are bare in winter, during which season the struggle for existence is most severe, and even the slightest disadvantage may prove fatal. Equally important, probably, has been the permanence of favorable conditions in the tropics, allowing certain groups to continue dominant for long periods, and thus to carry out in one unbroken line whatever development of plumage or color may once have acquired an ascendency. Changes of climatal conditions, and preëminently the Glacial epoch, probably led to the extinction of a host of highly developed and finely colored insects and birds in temperate zones, just as we know that it led to the extinction of the larger and more powerful mammalia which formerly characterized the temperate zone in both hemispheres. This view is supported by the fact that it is among those groups only which are now exclusively tropical that all the more extraordinary developments of ornament and color are found. The local causes of color will also have acted best in regions where the climatal conditions remained constant, and where migration was unnecessary; while whatever direct effect may be produced by light or heat will necessarily have acted more powerfully within the tropics. And, lastly, all these causes have been in action over an actually greater area in tropical than in temperate zones, while estimated potentially, in proportion to its life-sustaining power, the lands which enjoy a practically tropical climate (extending as they do considerably beyond the geographical tropics) are very much larger then the temperate regions of the earth. Combining the effects of all these various causes we are quite able to understand the superiority of the tropical parts of the globe, not only in the abundance and variety of their forms of life, but also as regards the ornamental appendages and vivid coloration which these forms present.

THE SEVEN TOWNS OF MOQUI.

BY E. A. BARBER.

AS early as the year 1540, Don Pedro de Tobar, one of the first Spanish adventurers, was dispatched by Coronado to the "province of Tusayan" (the modern Moqui, situated in Arizona, in longitude 110° to 111° west, and latitude 35° to 36°